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POPULATION STRUCTURE OF THE *ASTHENES FLAMMULATA* SUPERSPECIES (AVES: FURNARIIDAE)

François Vuilleumier[1]

INTRODUCTION

While conducting a survey of speciation phenomena in twenty-five genera of Andean birds, I found that the existing classifications of these birds were often insufficient for my purposes. I had to undertake systematic studies in each genus before I could proceed to an analysis of species formation. In view of the groundwork already laid by Hellmayr, Chapman, Zimmer, Peters, and others, it may seem surprising that a student of speciation should find it necessary to do so much systematic work. However, these earlier systematists were primarily concerned with the purely formal aspects of assigning samples to species and subspecies, rather than interested in the process of speciation; their works contain little information on population structure (in the sense of Mayr, 1959:294) or species relationships. My own taxonomic work on Andean birds was designed to fill this gap.

This is the first in a proposed series of papers on these Andean birds. My purpose has been to gain an understanding of the process of speciation in each genus sampled through study of population structure and interspecies relationships, and then to synthesize this information, arriving at a general picture of speciation phenomena in Andean birds. In the present paper, an effort has been made to uncover the evolutionary relationships of the component members of the *Asthenes flammulata* superspecies by means of an analysis of the distribution and geographical variation of these spinetails.

This study was undertaken at the Museum of Comparatize Zoology of Harvard University. My investigations were based largely on

[1] Research Fellow, Department of Ornithology, American Museum of Natural History, New York, New York 10024.

the collections of this institution, but I have also examined specimens from other museums. When referring to individual specimens, the following abbreviations are used: MCZ = Museum of Comparative Zoology; ANSP = Academy of Natural Sciences of Philadelphia; CM = Carnegie Museum, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; MVZ = Museum of Vertebrate Zoology, Berkeley; MP = Muséum National d'Histoire Naturelle, Paris.

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THE *ASTHENES FLAMMULATA* SPECIES GROUP

The genus *Asthenes* Reichenbach, 1853, consists of about 18 species of small spinetails (Furnariidae) living in western and

southern South America. At least four species groups can be recognized in *Asthenes*. Since this arrangement of the genus will be published elsewhere, it is sufficient to mention here that what I call the *Asthenes flammulata* species group comprises four nominal species: *Asthenes flammulata* (Jardine), *A. virgata* (Sclater), *A. maculicauda* (Berlepsch), and *A. urubambensis* (Chapman).

These four forms were considered full species by Hellmayr (1925), Peters (1951), and de Schauensee (1966). They all have a diagnostic pattern of streaking — a narrow stripe along the feather shaft contrasting with the remainder of the feather.

Within the *A. flammulata* species group, *A. urubambensis* can be diagnosed by the combination of a lack of streaking on the dorsum and a lack of rufescent color on the forehead and crown. Furthermore, *A. urubambensis* is sympatric with two of the three other nominal species of the *flammulata* species group: with *A. flammulata* in Peru (see Zimmer, 1930:345) and with *A. maculicauda* in Bolivia (see Bond and de Schauensee, 1942:334). There is therefore no doubt that *A. urubambensis* is a good biological species.

THE *ASTHENES FLAMMULATA* COMPLEX

The other three nominal species of the *A. flammulata* species group can be described collectively as the *A. flammulata* complex. They are morphologically rather similar to one another, and are largely allopatric, although there are two apparent exceptions: (1) in southern Peru ("contact" between *virgata* and *maculicauda*) and (2) in central Peru (alleged sympatry between *flammulata* and *virgata*).

Sympatry

Asthenes virgata was described by Sclater, in 1874, on the basis of one specimen collected by Jelski in "Junin," in the Andes of central Peru. In 1930, M. A. Carriker, Jr., secured five specimens of *A. virgata* in the Rock Forest area west of Lake Junín (Bond, 1945:33; 1956:245). Although Jelski did not give precise locality data, it is possible that "Junin" refers to the village of that name situated southeast of the lake at the edge of the flat depression forming the present-day Lake Junín and adjoining marshes (see Fig. 1). Junín and Rock Forest are about 50 km apart.

These are the only published localities where *A. virgata* has been taken, at least to my knowledge. However, C. Koford collected a single female *Asthenes* in the Department of Puno, southern Peru, in 1951 (MVZ 124302). This bird is morphologically much closer

FIG. 1. Collecting localities of the *Asthenes flammulata* complex.

to the geographically distant *A. virgata* from central Peru than to its nearest neighbor, *A. maculicauda.* As far as I know, this specimen has not been previously reported in the literature, although it was known to Zimmer, who identified it as *A. virgata* (pencilled comment on the label).

"Contact" between *A. virgata* and *A. maculicauda* appears possible when the collecting localities of Koford's specimen of *virgata* and of the northernmost record of *maculicauda* are examined. Koford's bird was collected eight miles SSW of Limbani at 15,250 feet (label data). The northernmost specimen of *maculicauda* appears to be a bird collected by Carriker at Huancarani, 13,000 feet (ANSP 103442). According to Bond (1945:19), Huancarani is "about ten miles above Limbani." Limbani is a village on the left (west) bank of the valley, and is accessible by only one road or trail from the southwest. Thus it is likely that "above Limbani" and "SSW Limbani" are very close to each other (Fig. 1). However, even if these two localities are not separated by a significant linear distance, they are separated by an altitudinal gap of 2250 feet (about 700 m). There is thus no direct evidence for sympatry between *A. virgata* and *A. maculicauda,* but in view of their morphological differences, their sympatry in southern Peru would not be surprising.

Sympatry between *A. virgata* and *A. flammulata* in central Peru was made apparent by the mention of four specimens of *A. flammulata taczanowskii* collected at Rock Forest by Dorst (1956: 268). But as I shall show below, Dorst's specimens are actually referable to *virgata;* sympatry is therefore non-existent, since only one taxon occurs at Rock Forest.

Geographical Variation

Altogether about 140 specimens have been examined from localities covering the entire range of the three nominal species of the *A. flammulata* complex (Fig. 1). Specimens were grouped into "populations," which are mapped on Figure 2. The grouping was based on several considerations, primarily (a) whether or not certain localities appeared to be isolated from others, thus representing potential interruptions in gene flow, and (b) whether or not the birds from several more or less adjacent localities were morphologically uniform. Thus specimens from the widely-spaced collecting locatities of the Eastern Andes of northern and central Peru were considered as one "population" (H) because of their considerable

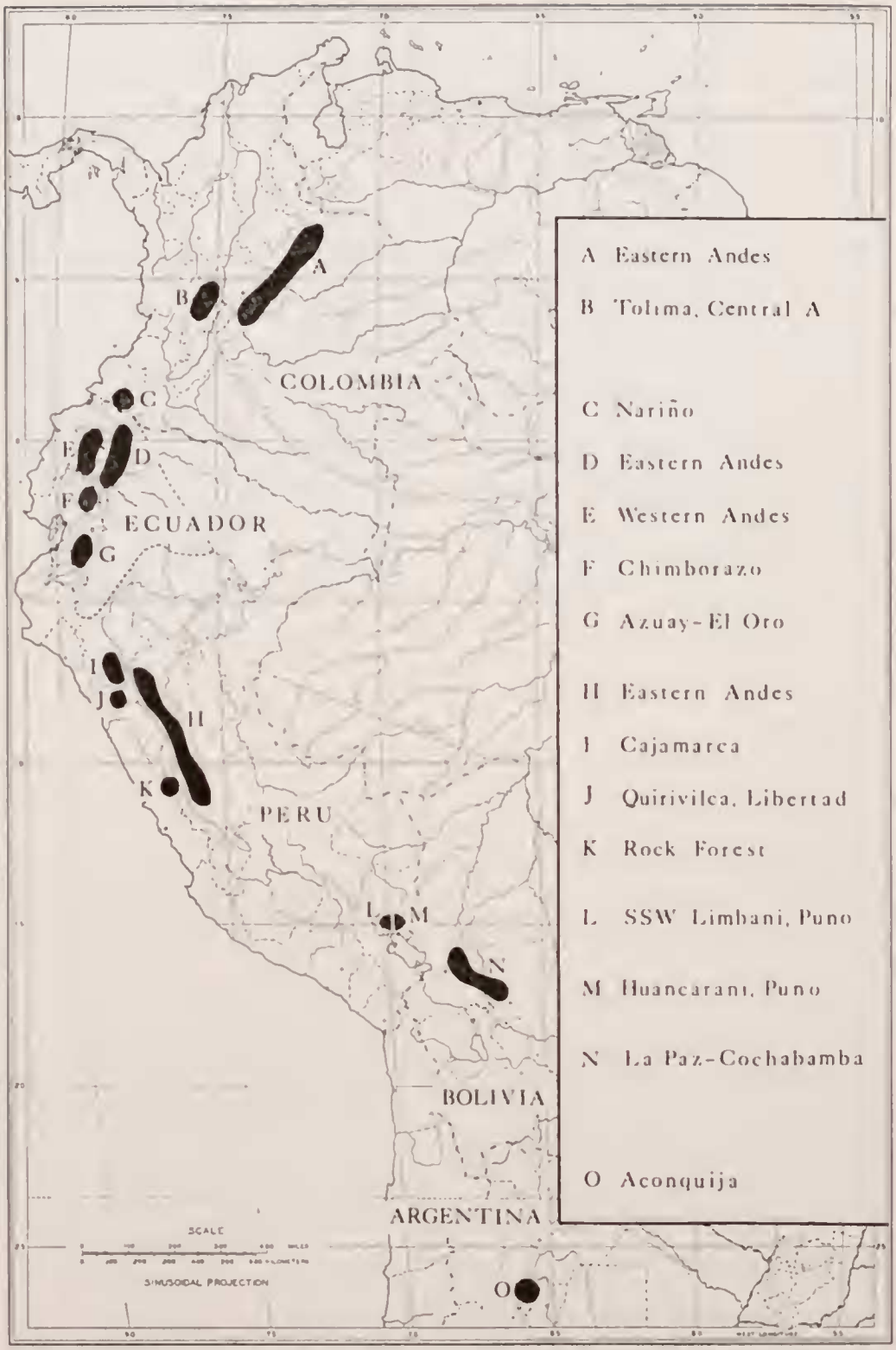

FIG. 2. The populations of the *Asthenes flammulata* complex.

morphological uniformity; on the other hand, those from the Western Andes of northern Peru were placed in two "populations" (I and J) because of geographical variation in some characters.

Despite this grouping into populations, the samples available were small. Under these circumstances, statistical treatment of the mensural characters was not attempted.

TABLE 1

Geographical variation of bill length in the *Asthenes flammulata* complex

Populations	Range of mean bill length (in mm)	
	Males	Females
Colombia, Ecuador northern Peru (A-L)	17.0-17.9	16.0-19.0
Southern Peru, Bolivia, northern Argentina (M-O)	15.0-16.5	15.3-15.5

TABLE 2

Geographical variation of tarsus length in the *Asthenes flammulata* complex

Population	Tarsus length of males (in mm)			Tarsus length of females (in mm)		
	Range	(Mean)	N	Range	(Mean)	N
A	24.0-27.0	(25.3)	3	23.0-24.0	(23.7)	3
B	25.0-27.0	(25.9)	11	23.5-26.0	(24.7)	6
C						
D	24.0-27.0	(25.8)	12	25.0-25.5	(25.1)	4
E	25.0-26.0	(25.6)	9	23.0-26.0	(24.8)	14
F	25.0-25.5	(25.2)	3		24.0	1
G	24.5-26.0	(25.3)	2	24.0-25.0	(24.5)	2
H	23.0-24.0	(23.9)	7	23.0-24.0	(23.8)	4
I	23.0-24.0	(23.0)	2		25.0	1
J	24.0-25.0	(24.3)	3			
K	23.0-27.0	(24.6)	7	23.0-24.0	(23.5)	2
L					26.0	1
M		23.0	1			
N	22.0-24.0	(22.8)	4	22.0-22.0	(22.0)	2
O	22.0-23.5	(22.8)	3	20.0-21.5	(20.8)	2

Mensural characters. Geographical variation in bill length, tarsus length, and wing length, respectively, is summarized in Tables 1 and 2 and in Figure 3. Populations M, N, and O (from southern Peru to northern Argentina) are distinguishable from their neighboring populations by a gap (step) in either absolute size or in mean length of all three characters. By contrast, steps between any two of the populations from A through L (Colombia to southern Peru) are much less significant (see especially Fig. 3).

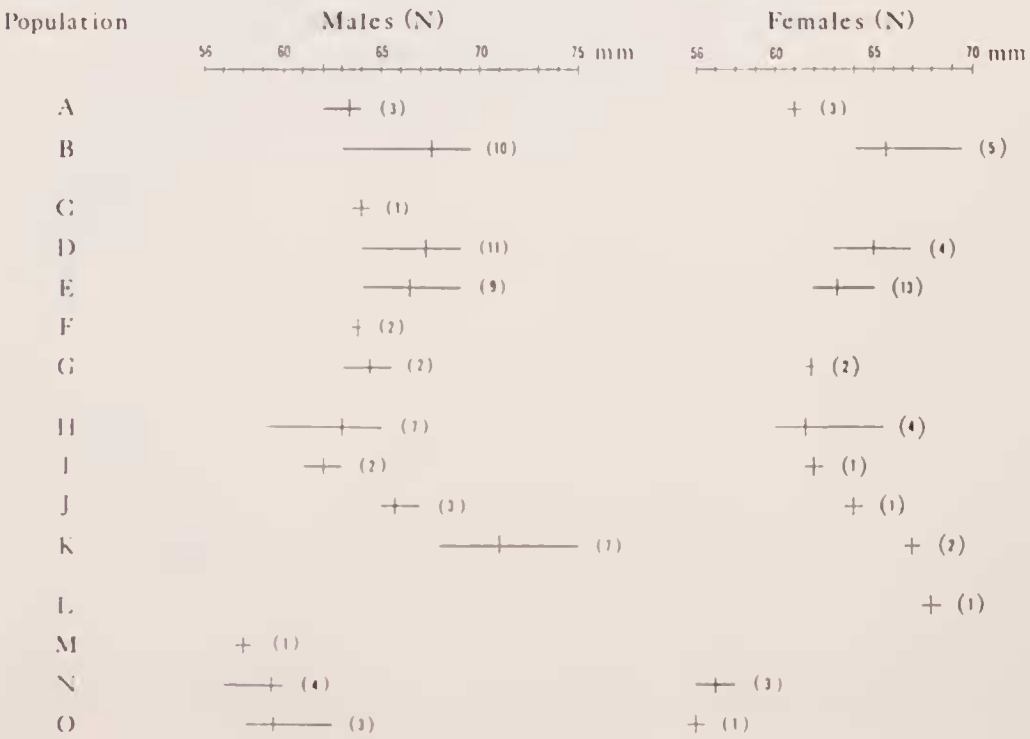

FIG. 3. Geographical variation of wing length in the *Asthenes flammulata* complex.

From the variation in mensural characters, one might conclude that the *A. flammulata* complex consists of two units, each an interbreeding species. The first would include populations A through L (nominal species *A. flammulata* and *A. virgata*), and the second populations M through O (nominal species *A. maculicauda*).

Color characters. Geographical variation in the color of the gular patch, the color of the forehead, the amount of streaking on the abdomen and crissum, the color of the rump and upper tail coverts, and the markings of the median pair of rectrices is summarized in Table 3. Variation in wing pattern is illustrated in Figure 4. Detailed notes on variation in these characters are included in Appendix I; only the major trends will be discussed here.

TABLE 3

Geographical variation of some color characters in the *Asthenes flammulata* complex

Character	Population														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Gular patch	RO	RO	PO	PO	PO	PO	PO	Y	Y	Y	RO	RO	A	A	A
Forehead	Ru	Ru	Sr	Sr	Sr	Sr	Sr	Sy	Sy	Sy	Sy	Sy	Ru	Ru	Ru
Crissum	St	St	St	St	St	St	St	St	St	St	Bu	Bu	Bu	Bu	Bu
Rump	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	U	U	HS	HS	HS
Central pair rectrices	Un	Un	Un	Un	Un	Un	Un	Un	Un	Un	Un	M?	M	M	M

Symbols:

Gular patch: RO = Rich ochraceous; PO = Pale ochraceous; Y = Yellowish; A = Gular patch undifferentiated

Forehead: Ru = Rufous; Sr = Streaked with rufescent; Sy = Streaked with yellowish

Crissum: St = Streaked; Bu = Buffy, unstreaked, or with obsolescent streaks only

Rump: HS = Heavily streaked; U = Unstreaked

Central pair rectrices: Un = Unmarked; M = With irregular markings

Characters such as the color of the gular patch, the color of the forehead, and the intensity of streaking on the underparts vary rather gradually. There is a trend, from north to south, toward a decrease both in saturation of pigmentation and in the amount of streaking. Exceptions to this trend are provided by populations K and L (gular patch color) and populations M, N, and O (forehead color).

The other characters seem to vary more discontinuously. These patterns of discontinuous variation permit one to distinguish morphologically several populations or groups of populations within the *A. flammulata* complex. The best-marked group includes populations from southern Peru to northern Argentina (M, N, O). These birds are differentiated from their neighboring populations by gular patch color, forehead color, and streaking on the rump. The steps observed in the variation of these color characters correspond to those noted in the mensural characters.

Other groups of populations can also be separated morphologically, but on the basis of fewer characters. Thus the birds of populations A and B (Colombia) can be distinguished by the color of the gular patch and the color of the forehead. Similarly, birds from populations K and L (Rock Forest and SSW Limbani) are separable from others by the color of the gular patch and the general absence of streaks on the rump and upper tail coverts (if these streaks are present, they are obsolescent).

However, it must be pointed out that such a neat separation of populations cannot be done using some other characters. For example, populations K and L are not distinguishable from populations M, N, and O on the basis of color or streaking of the underparts. Also, populations K and L are indistinguishable from populations H through J in forehead color.

When variation in color characters (as in mensural characters) is considered as a whole, the *A. flammulata* complex appears to comprise two units. Geographical variation within populations A through L, and within M through O, could be interpreted as that normally to be found in an interbeeding species. However, unlike what is found in mensural characters, the gap in color characters separating populations A-L and M-O does not seem to be as well marked as the gap separating some populations within A-L.

Population Structure

The dual type of geographical variation (gradual and discontinuous) exhibited by the *A. flammulata* complex is often found in

a single polytypic species with a partially continuous and partially discontinuous range.

Although the number of specimens examined is not large enough to reach definite conclusions, it seems probable that the gradual size trends (especially in tarsus and wing length) detected are positively correlated with altitude. Thus the largest birds seem to live at slightly higher elevations (in north-central Ecuador and central to southern Peru) than the smallest birds (in southern Ecuador and northern Peru. Altitudinal variation in Andean birds has been demonstrated by Traylor (1950) and myself (unpublished). However, the correlation of increase in size with increase in altitude is not the only possible one. In Peruvian birds, for example, the north-south size increase along the Western Andes could be due to latitude or aridity (Hamilton, 1961), rather than to altitude.

The decrease in the intensity of pigmentation from north to south cited earlier is also detectable in several species belonging to other Andean genera (unpublished). Such variation may be correlated positively with the decrease in rainfall along the Andes from north to south (see, e.g., Troll, 1959); thus it corresponds to Gloger's rule.

The apparent trends of gradual geographical variation are clearest in populations A through L, which have the earmarks of representing a single species, as already noted. It is, therefore, of interest that populations M-O, which are separated from populations A-L by a marked morphological gap in some characters, have a very different type of population structure. Although populations M, N, and O are apparently disjunct (see Fig. 2), the birds I have examined are all remarkably uniform and display only slight geographical variation — in wing length, for example (see Fig. 3). This lack of significant geographical variation can be explained either by free gene flow, or by recency of occupation of the vast geographical range, or possibly by both. Whatever the reason, the differences in population structure would tend to confirm the previous impression of specific distinctness between populations A-L (*flammulata-virgata*) and M-O (*maculicauda*). Since, as noted previously, there is no apparent barrier between the two groups of populations in southern Peru, I would conclude that their differentiation does not reflect the result of evolution *in situ* (unless, of course, a barrier once present has subsequently been removed). This question cannot yet be answered, but the problem will be taken up in a later paper in this series.

To study the possible correlation between discontinuous variation and geographical barriers in the *A. flammulata* complex, we must turn to populations A-L, ranging from Colombia to southern Peru.

Discontinuous Variation and Geographical Barriers

The presence of a geographical barrier between avian populations does not *ipso facto* mean that gene flow between the isolates is interrupted. Similarly, the fact that geographical isolates are not differentiated morphologically, or are so only slightly, does not necessarily mean that gene flow takes place between them. Consequently, statements made in the following paragraphs about differentiation and gene flow across barriers must be taken, not as expositions of known facts, but as cautious expressions of probabilities.

The correlations between morphological differentiation and geographical barriers in populations A-L of the *A. flammulata* complex will be mentioned in geographic sequence from north to south.

(1) In Colombia, the birds from the Eastern Andes (*multostriata*) are separated from those of the Central Andes (*quindiana*) by the Magdalena Valley (Fig. 5). Morphological differences between these two isolated populations (A and B on Fig. 2) include wing length, the width of the streaks on the underparts, the presence or absence of a slight buffy wash on the undertail coverts, the extent of the gular patch, and the intensity of the coloration of the forehead. The two populations are certainly sufficiently differentiated to be recognized taxonomically, although they are more similar to each other than they are (either as a group or separately) to populations farther south in Colombia and Ecuador (C-G).

(2) Between the Eastern or the Central Andes of Colombia and the Andes of Nariño in southern Colombia is an apparent distribution gap (Fig. 5). The only specimen from Nariño (C) I have seen (Mayasquer, ANSP 149893) appears somewhat intermediate in both postocular stripe and cheek color between Colombian birds (A-B) and Ecuadorian specimens (D-G). However, since these differences are slight, it is not possible to assess the real extent of intermediacy. In other characters, furthermore, the Nariño specimen falls fully within the range of variation of Ecuadorian specimens. The vast geographical gap between Colombian populations A-B and southern Colombian-Ecuadorian populations C-G is therefore correlated with a relatively well-marked morphological gap. Taxonomic recognition of populations C-G (subspecies *flammulata*) is thus warranted.

(3) The Interandean Depression of Ecuador (Fig. 5) is a low and relatively dry region separating the Eastern from the Western Andes. Only a slight difference in wing length and tarsus length

between birds of the Eastern (D) and Western (E) Andes was detected, suggesting only a slight restriction in gene flow; taxonomic subdivision within populations C-G (*flammulata*) would be unjustified.

(4) There is a gap between the northern Peruvian populations of the Eastern (H: *taczanowskii*) and Western (I: *pallida*) Andes and those of southern Ecuador (G). For population H, the gap corresponds to the eastward bend of the Marañon River; for population I it corresponds to the generally low altitude and small area of suitable habitat of the Andes of northwestern Peru (Northern Peruvian Low: Fig. 5). The morphological differences between Ecuadorian and Peruvian birds are not large. They include the intensity of streaking on the underparts and the extent of rufous on tail feathers. The lack of major differences suggests either some gene flow over the gap, or that the separation of Ecuadorian from Peruvian birds is of recent origin.

(5) The Upper Marañon Basin (Fig. 5) separates the northern Peruvian populations of the Eastern Andes (H: *taczanowskii*) from those of the Western Andes (I and J: *pallida*). Only slight morphological differences can be noted between them, however: these include characters such as tarsus length, wing length, and intensity of streaking of the rump and upper tail coverts. I could find no differences in the other characters examined. In view of this minor morphological differentiation, subspecific separation of the two populations may not be warranted; *pallida* may be considered a synonym of *taczanowskii*. As Bond (1945:32) has remarked, *pallida* "is not a very well-marked race."

(6) The specimens collected in the Rock Forest area of central Peru (K: *virgata*) are distinguishable morphologically from the birds living in both the Eastern (H) and Western (I, J) Andes. The differences are in wing length, color of gular patch, color of central pair of rectrices, amount of streaking on rump and upper tail coverts, wing pattern, and color of the lower abdomen and crissum. These differences are better marked between Rock Forest specimens (K) and birds from the Eastern Andes (H), than between Rock Forest birds and specimens from the Western Andes (I, J). An approach to Rock Forest birds is clearly seen in Western Andean birds (especially population J) in size (Fig. 3) and in wing pattern (compare nos. 5 and 6 on Fig. 4).

Geographical isolation between Rock Forest birds (*virgata*) and Eastern Andean birds (*taczanowskii*) is apparently provided by the Lake Junín Basin (Fig. 5). But since the first specimen of *virgata* may have come from "Junin" in the center of the basin, a more

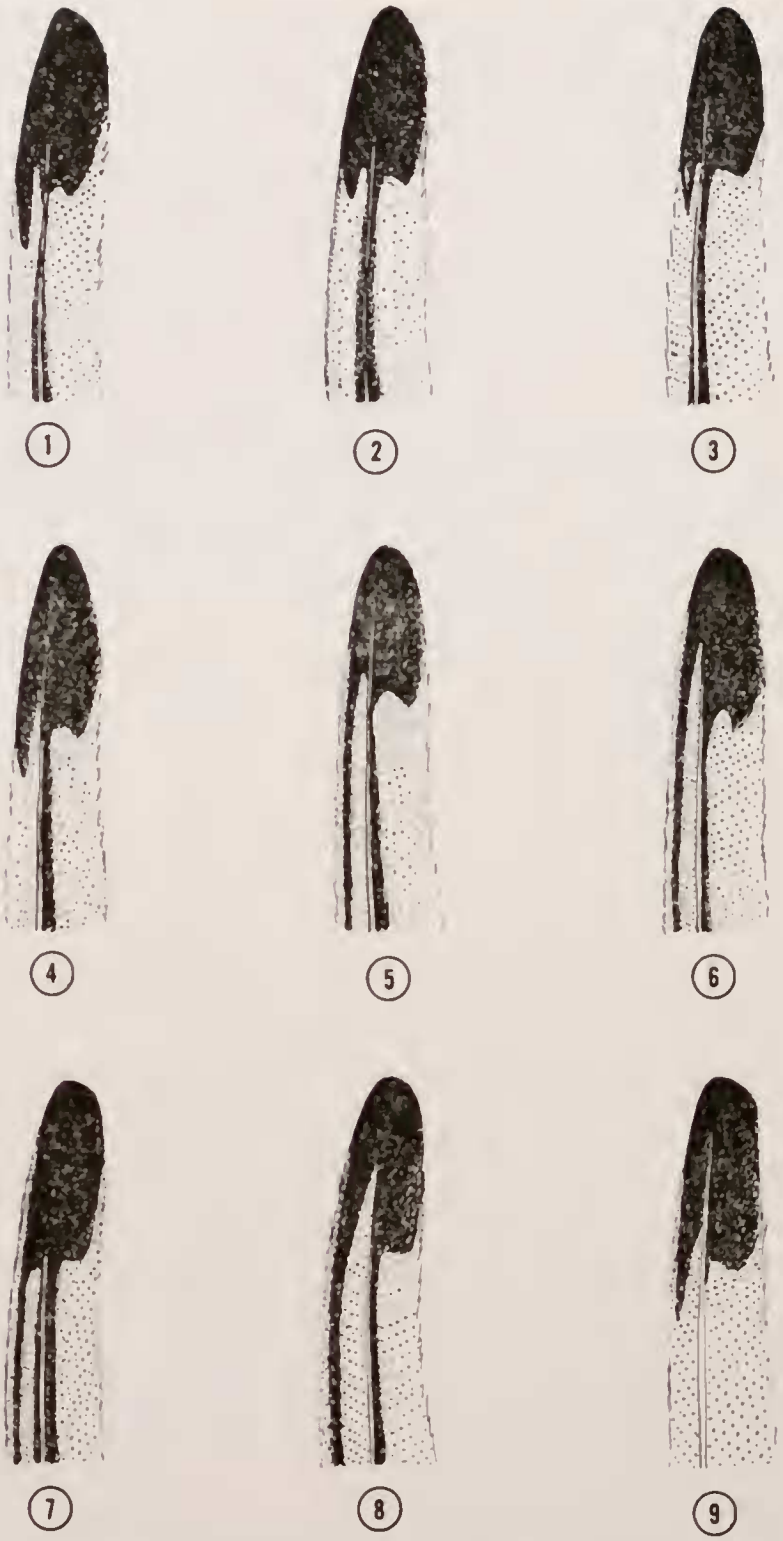

FIG. 4. Geographical variation of wing pattern in the *Asthenes flammulata* complex. The feather illustrated is the sixth outer primary.

Key: 1 = Volcán Pichincha, Ecuador; 2 = Huánuco, northern Peru; 3 = Maraynioc, central Peru; 4 and 5 = Quirivilca, Libertad, northern Peru; 6 = Rock Forest, central Peru; 7 = SSW Limbani, southern Peru; 8 and 9 = Incachaca, Cochabamba, Bolivia

likely barrier may be the high Andes farther east. In any event, although the barrier is not clear-cut at present, morphological differentiation is fairly sharp.

Isolation between Rock Forest birds (*virgata*) and populations found farther north along the Western Andes (J: *"pallida"*) is not clear. The closest specimens come from Quirivilca, Libertad, about 375 km from Rock Forest. No specimens are known to me from the intervening area, although apparently suitable habitats occur there. A possible barrier might be the Santa River Canyon, which makes a cut across the Andes between the Cordillera Blanca and the Andes of Libertad.

(7) The vast Andean area between central and southern Peru (about 800 km) seems to represent a distribution gap in the range of the *A. flammulata* complex. However, suitable habitat occurs there, and further collecting might reveal the presence of the complex there (? on Fig. 5). The specimen from SSW of Limbani is practically identical with Rock Forest specimens (*virgata*), except in the pattern of the central pair of rectrices.

Taxonomic Conclusions

The classification of Hellmayr (1925), Peters (1951), and de Schauensee (1966) is as follows. Colombian, Ecuadorian, and northern Peruvian populations (A-J) are treated as one species, *Asthenes flammulata.* The two disjunct populations from central and southern Peru (K and L) would constitute a second species, *A. virgata.* Finally, the populations from southern Peru to northern Argentina (M, N, O) make up a third species, *A. maculicauda.* A slight modification of this classification was made by Bond and de Schauensee (1942:334), who considered *maculicauda* a subspecies of *flammulata.* (Later, however, Bond, 1945:32, cited *maculicauda* as a full species without any comment.) This classification finds justification in the fact that there is a morphological and partial geographical gap between *flammulata* and *virgata* (see (6) above), and because there is a morphological gap between *flammulata-virgata* and *maculicauda.*

I believe, however, that the evidence presented in this paper allows one to construct a classification of the *A. flammulata* complex which is at the same time a simplification and an improvement over the older scheme.

The *Asthenes flammulata* complex constitutes a superspecies (*sensu* Mayr, 1963:501) having two component species. The first

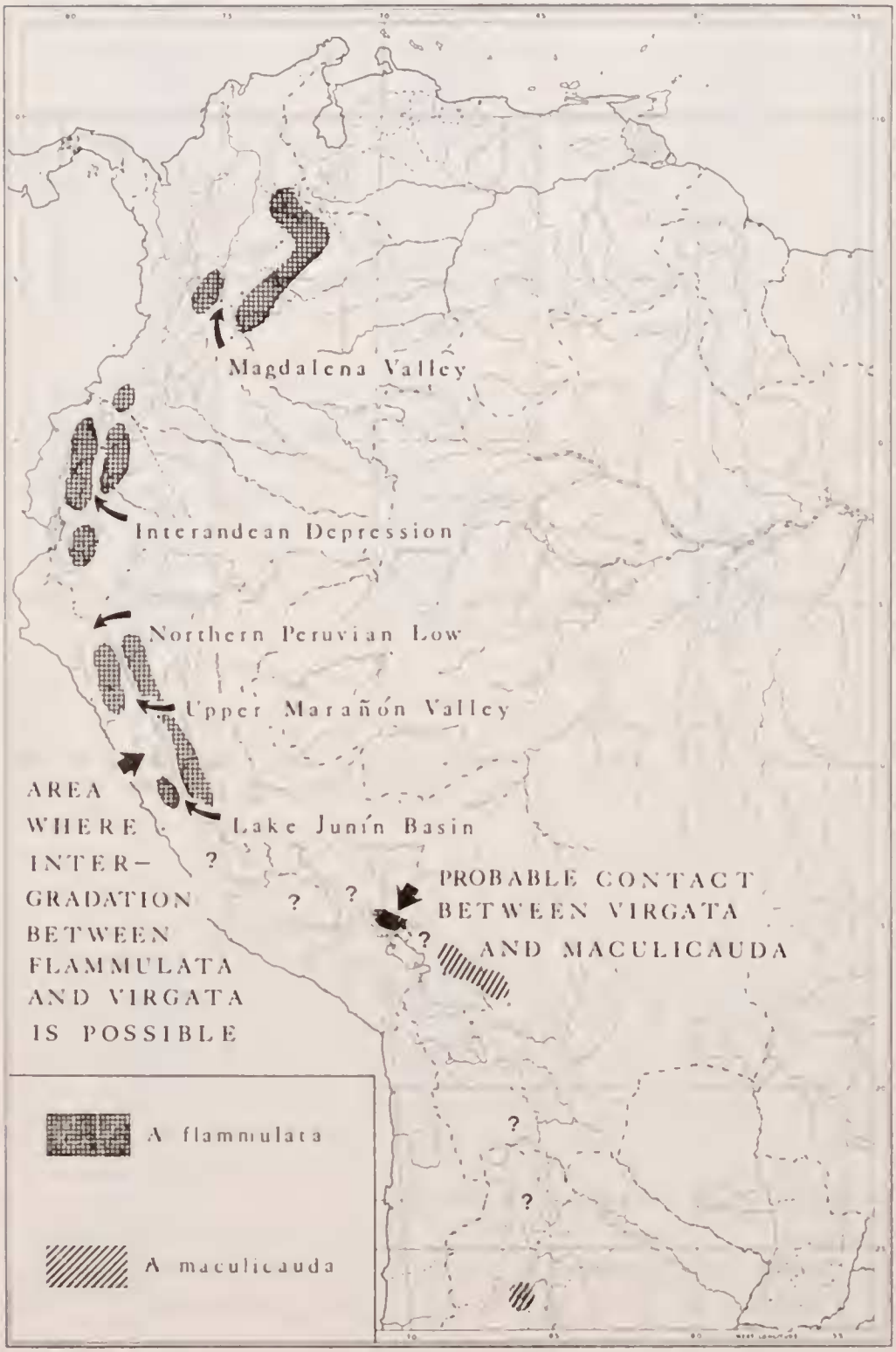

FIG. 5. Taxonomic and evolutionary interpretation of distribution and geographic variation in the *Asthenes flammulata* superspecies.

species is composed of several isolated and semi-isolated populations ranging from Colombia to southern Peru (*Asthenes flammulata*). Fully isolated populations of *A. flammulata* which have reached a moderate to marked degree of differentiation (incipient species) are the Colombian *multostriata* and *quindiana*. These two isolates are perhaps best considered as a subspecies group with two subspecies. The specimens from Rock Forest and SSW Limbani fall within the range of variation of a single taxon (*virgata*).[1] Some gene exchange between Rock Forest birds and birds farther north in the Western Peruvian Andes is suggested by the variation of characters such as wing length (Fig. 3). I consequently recommend that *virgata* be treated as a subspecies of *A. flammulata*.

The second component species of the *A. flammulata* superspecies, *Asthenes maculicauda,* is composed of three apparent isolates (M, N, O), but it does not exhibit much geographical variation.

The taxa of the *A. flammulata* superspecies and their relationships can be listed as follows:

Asthenes flammulata superspecies (two component species which may have achieved reproductive isolation)

(1) *Asthenes flammulata* (Jardine, 1850)

(a) Colombian subspecies group (one or two incipient species): *A. flammulata multostriata* (Sclater, 1858), *A. flammulata quindiana* (Chapman, 1915)

(b) Ecuadorian-Peruvian subspecies group (two or three incipient species): *A. flammulata flammulata* (Jardine, 1850); *A. flammulata taczanowskii* (Berlepsch and Stolzmann, 1894; includes *A. f. pallida* Carriker, 1933); *A. flammulata virgata* (Sclater, 1874)

(2) *Asthenes maculicauda* (Berlepsch, 1901)
Shows insignificant geographical variation

SUMMARY

The Andean spinetails of the *Asthenes flammulata* complex include three nominal species, *flammulata, virgata,* and *maculicauda,* which, together with a fourth, *A. urubambensis,* constitute the *A. flammulata* species group.

[1] The specimens reported by Dorst (1956) as *A. flammulata taczanowskii* from Rock Forest are therefore referable to *virgata*.

Specific status of *A. urubambensis* is shown by sympatry with two nominal species of the *A. flammulata* complex and by morphological distinctness.

The evolutionary relationships of the three nominal species of the *A. flammulata* complex were analyzed by a study of geographical variation and its correlation with geographical barriers. Geographical variation is largely discontinuous in populations ranging from Colombia to southern Peru (nominal species *flammulata* and *virgata*). By contrast, populations from southern Peru to northern Argentina show great morphological uniformity (nominal species *maculicauda*).

It is concluded that the *Asthenes flammulata* complex is best considered as a superspecies with two component species. The first species, *A. flammulata*, contains several isolated groups of populations (incipient species) showing various degrees of morphological differentiation across barriers. *A. virgata* should be included as a subspecies of *A. flammulata*. The second species, *A. maculicauda*, may come in contact with *A. flammulata virgata* in southern Peru. Gene exchange between the two species is not suggested, but there are only two specimens on which to base a decision.

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APPENDIX I: NOTES ON GEOGRAPHICAL VARIATION IN NON-MENSURAL CHARACTERS

Gular patch. The gular patch varies in color intensity from whitish and yellowish to rich ochraceous, and in extent from a small, roughly triangular patch more or less restricted to the chin, to a wider patch comprising also the throat and upper chest.

Colombian specimens (populations A and B) have a richly ochraceous gular patch. Central Andean birds (B) have a rather broad patch, while in Eastern Andean birds (A) it is more restricted.

Ecuadorian specimens and the Nariño specimen from Mayasquer (populations C-G) have relatively narrow and more or less triangular gular patches, varying from whitish-yellow to pale ochraceous.

Peruvian specimens (populations H-J) have a broad, ill-defined gular patch merging into the upper chest. The patch varies in color from dirty white to yellowish-cream. Usually the chin area is somewhat paler than the throat. Some specimens of Ecuadorian birds (e.g. MCZ 199104, female, and MCZ 199099, male) have a more ill-defined gular patch than do most other Ecuadorian specimens, thus showing an approach to Peruvian specimens.

Peruvian specimens from Rock Forest and SSW Limbani (K and L) have a relatively small, well-defined gular patch, usually of a rich ochraceous color.

Specimens from southern Peru to northern Argentina (M, N, O) lack a buffy-ochraceous gular patch: the gular area is of about the same color as the chest.

Forehead color. In Colombian specimens from both the Eastern and Central Andes (A and B) the forehead is an almost solid rufous, especially in males. The forehead of most Ecuadorian specimens (C-G) is streaked with rufescent, although in some birds (e.g. MCZ 138553) it is a solid rufous. In Peruvian birds from populations H, I, and J the forehead streaks are less rufescent, more yellowish, but here again at least one specimen (FMNH 65849, male) has a rufous forehead, where the streaks almost join to form a solid color. In Peruvian specimens from Rock Forest and SSW Limbani (K-L) the streaks are relatively yellowish, not very rufescent. Finally, specimens from southern Peru, Bolivia, and northern Argentina (M, N, O) have rufescent foreheads, distinctly more pigmented than those of Peruvian birds in general, and of Rock Forest-SSW Limbani birds in particular.

Coloration of underparts. Colombian specimens are the most heavily streaked; Bolivian and Argentine specimens are almost unstreaked. The birds from Rock Forest, SSW Limbani, Huancarani, Bolivia, and northern Argentina (K-O) are the least streaked of all populations within the *Asthenes flammulata* complex. The additional fact that in the birds from these same populations the lower abdomen and crissum are buffy with obsolescent streaks, rather than whitish with rather conspicuous streaks, permits one to distinguish them immediately from all other populations (A-J). There is, in particular, a rather well marked difference in streaking intensity between the crissum of Peruvian birds from the Eastern (H) and Western Andes (I, J), and that of birds from Rock Forest (K).

Specimens from southern Peru to northern Argentina (M, N, O) have, alone among the populations of the *A. flammulata* complex, a series of ill-marked streaks on the chest converging toward the center to form a ring.

Color of rump and upper tail coverts. The birds from Rock Forest and SSW Limbani (K and L) have slight or obsolescent streaking on the rump and upper tail coverts. (This was already noticed by Bond [1956: 245] for Rock Forest specimens.) By contrast, specimens from all other populations have generally much heavier streaking on the rump and upper tail coverts. These streaks are relatively well marked in Peruvian populations H, I, and J, as well as in Peruvian, Bolivian, and Argentine populations M, N, and O. Rock Forest and SSW Limbani (K-L) specimens are thus distinguishable as a group from neighboring populations.

Wing pattern. The primaries of birds in all populations are more or less rufous with a dark brown to blackish tip. I have studied interpopulation variation in pattern by comparing the patterns of the sixth outer primary, which was chosen arbitrarily.

Except for a few Colombian specimens, which have only a relatively narrow rufous edge to both vanes of the sixth primary, in most other specimens (including those from Colombia) the tip of the feather is more or

less wholly dark brown, while its base is rufous (see Fig. 4, Nos. 1, 2, 3, 4, and 9).

The most significant population variation is in the presence or absence of a thin dark brown stripe along the outer vane of the primary (compare Nos. 4 and 5 of Fig. 4, for example). This pattern is seen in some specimens from Quirivilca, Libertad (population J), every specimen from Rock Forest (K), the single specimen from SSW Limbani (L), and most specimens from southern Peru to northern Argentina (M, N, O). The presence of the two major patterns in the Libertad and Cochabamba populations is illustrated in Fig. 4 (Nos. 4 and 5, and Nos. 8 and 9, respectively).

Marking of rectrices. Analysis of variation in this character is difficult because a rather large number of specimens have one or several rectrices in molt or missing and because many specimens have extremely worn rectrices. Nevertheless, the detectable variation appears as follows.

There is a tendency for Peruvian specimens (including the specimen from SSW Limbani, but excluding Rock Forest specimens) to have more rufous on outer tail feathers than do Ecuadorian or Colombian specimens.

Rock Forest specimens lack entirely or almost entirely the narrow rufescent or pale brownish outer edge to the outer vane of the central pair of rectrices, which is present in specimens from all other Peruvian localities including SSW Limbani.

In birds from southern Peru to northern Argentina (M, N, O), the central pair of rectrices is marked with irregular dark brown designs on a rufous or rufescent background. No other specimen from anywhere in the range of the *Asthenes flammulata* complex has similar markings on the median rectrices, with one exception: in the central pair of rectrices of the specimen from SSW Limbani, the outer part of the outer vane is rufescent, with a thin and irregular dark brown line running alongside the rufescent color. This pattern, although reminiscent of that found in birds from populations M, N, and O, is not really similar to it.

In rectrices other than the central pair, a pattern reminiscent of the one found in specimens from southern Peru to northern Argentina (M, N, O) is noticeable in specimens from Rock Forest (ANSP 92428, ANSP 92427, MP CG1956 No. 942, MP CG1956 No. 940), as well as in other populations. But the number of specimens in which this pattern occurs tends to become smaller north of central Peru.